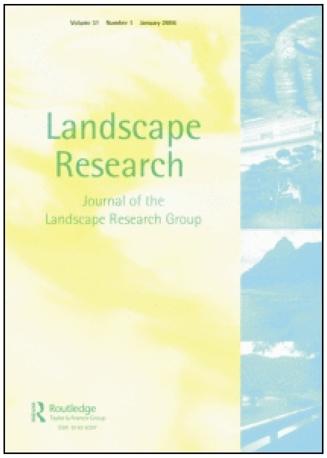

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The contribution of ecological science to the development of landscape ecology: a brief history

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The Contribution of Ecological Science to the Development of Landscape Ecology: a Brief History

Peter A. Quinby

Historically, ecologists have recognized the existence of four levels of ecological organization — the individual organism, the population, the community, and the ecosystem (Odum 1971). Recently, however, a new level of ecological organization has emerged with a focus on the ecology of the landscape (Forman & Godron 1981, Tjallingii & de Veer 1981, Naveh 1982, Risser *et al.* 1983, Naveh & Lieberman 1984, Forman & Godron 1986, Urban *et al.* 1987). In their discussion of the development of landscape ecology, Naveh & Lieberman (1984) and Forman & Godron (1986) emphasize the historical significance of the merging of such disciplines as geography, phytosociology, landscape architecture, and forestry. While the contribution of these disciplines to the development of landscape ecology cannot be denied, contributions from the field of ecology itself should also be fully acknowledged. The purpose of this review is, then, to show that landscape ecology has been significantly influenced by the development of the broader discipline of ecological science. Because there is no absolute beginning to the discipline of ecology and its various levels of integration (McIntosh 1985) and because of the multitude of contributions to this field, only some of the more notable basic and methodological contributions will be discussed.

The development of the biological sciences has proceeded according to the concept of integrative levels (Novikoff 1945, Rowe 1961). This concept was later renamed the levels-of-organization concept (Dansereau 1964, Blair 1964, Odum 1964, Macfadyen 1975). Novikoff (1945) provides an explanation of this concept:

"The concept of integrative levels of organization is a general description of the evolution of matter through successive and higher orders of complexity and integration. In the continual evolution of matter, new levels of complexity are superimposed on the individual units by the organization and integration of these units into a single system. What were wholes on one level become parts on a higher one. Each level of organization possesses unique properties of structure and behaviour which, though dependent on the properties of the constituent elements, appear only when these elements are combined in the new system. Knowledge of the laws of the lower level is necessary for a full understanding of the higher level; yet the unique properties of phenomena at the higher level cannot be predicted, *a priori*, from the laws of the lower level. The laws describing the unique properties of each level are qualitatively distinct, and their discovery requires methods of research and analysis appropriate to the particular level. These laws express the new organizing relationships . . ."

The distinct discipline of ecology did not arise until the late nineteenth century. However, observations and descriptions of ecological relationships had been made much earlier (Brewer 1960). Field observations of other species date back to the very origin of humans. Primitive human dependency on fishing, hunting, and food gathering required a detailed knowledge of habitat and seasonaility. Later, the development of agriculture required the application of ecological knowledge in order to manage crop plants and domestic animals.

The Greeks were the first to study biology systematically. Aristotle, the founder of biological science (Ramaley 1940), named many hundreds of organisms and grouped them according to his own scheme of classification. In the *Historia Animalium*, he classified animals partly on a morphological and physiological basis and in part on an ecological basis (Park 1945). Theophrastus, however, may be regarded as the first ecologist in history (Ramaley 1940). He delineated natural associations of plants and wrote about the relationship between these communities and their non-living environments and is credited with the founding of plant systematics. By the beginning of the Christian era, man had accumulated a good deal of practical knowledge. However, biology experienced a stagnation at that point and whatever knowledge was accumulated was largely lost to the Western world (Rickleffs 1973). Not until the seventeenth century in Europe was the study of the biological sciences revived and the term "ecology" was not coined until the 1800s, by Haeckel (1869).

Physiological ecology, the study of the relationship between the individual organism and the environment, underwent a major advancement when Galileo invented the hermetically sealed thermometer. The use of this instrument allowed the French naturalist Reaumur to correlate the early maturing of fruit and grain with higher mean daily temperatures for April, May, and June of 1734 compared to lower temperatures for those months of 1735 (Kendeigh 1974). Since the 1700s physiological ecology has continued to focus on the biochemical responses of individual organisms to energy and material changes. Of all the sub-fields of ecology, physiological ecology is by far the most advanced. This is primarily due to its longer history and particular relevance to fields of applied biology such as human and veterinary medicine and agriculture.

The responses of individual organisms to the environment determine the characteristics of a species' life history. The cumulative effects of these responses within a species make up the features of a population. The quantitative character of a population was first demonstrated in 1662 by Graunt, who has been called the father of demography (Cole 1958). He recognized the importance of representing birth rate, death rate, sex ratio, and age structure of human populations mathematically. In 1687, Leewenhoek made one of the first attempts to calculate a theoretical rate of increase for an animal species by counting eggs laid by female carrion flies (Egerton

Abstract

The emerging discipline of Landscape Ecology is described, and its historical development studied. Differences between European and North American practice are revealed and the discipline is seen to emerge as much from ecological studies as from geography, forestry and landscape architecture. An extensive list of references is given.

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1968). Buffon (1756) also contributed to the development of population ecology by recognizing that populations of humans, other animals, and plants are all subjected to the same controlling factors.

Creating controversy over the subject of demography, Malthus (1798) proposed that numbers of organisms increase geometrically whereas their food supply increases arithmetically. This lead Malthus to conclude that reproduction must eventually be checked by food depletion. These ideas were not new, but it was Malthus who brought them to general attention. Later, Velhurst (1838), a Belgian statistician, derived the logistic equation which described the course of population growth over time. This key work was, however, overlooked until modern times.

Contemporary population ecology cannot be understood without mathematics (Hutchinson 1978). Lotka (1925) first combined the concepts of energy transformation and population process into mathematical theory (Elton 1966). Volterra (1926) was also instrumental in developing theoretical mathematics to demonstrate the manner in which different populations of species interact. These new mathematics served as vital methodology for further advancement of population ecology and have contributed greatly to other sub-fields of ecology.

In the 1930s and based on the work of Lotka and Volterra, Nicholson (1933) and Gause (1935) conducted studies that focused upon interacting populations of predators and prey. This work stimulated much thinking about the factors that stabilize populations at particular levels and represented experimentation with simple communities.

The variety and interaction of populations within a common space make up communities. The origin of the modern concept of the ecological community has been traced back to the studies of August Grisebach (1838), a German botanist who recognized the plant formation as the fundamental feature of vegetation (Kendeigh 1974). A substantial contribution to the development of this idea was Darwin's concept of the 'web of life', which implied the interdependence of all organisms living within a community. Taking this interdependence concept one step further, Warming (1909) presented the idea that plant distribution is based on the heterogeneity of environmental influences. His studies of sand-dune vegetation were also important in laying the groundwork for the formal development of the concept of community succession, presented in what might be considered the first ecological textbook, *Oecology of Plants* (1909).

Greatly influenced by Warming, Cowles and Clements are credited with formulating two very central concepts in the early development of community ecology. Cowles (1899) did far more than any other to develop and describe the concept of succession (Tansley 1835). Also, in 1916, Clements defined the term "climax", which refers to the end product of succession or the mature community in dynamic equilibrium with the physical environment.

A dominant modern concern in the study of communities is the concept of stability. Whittaker (1975) asked, "How are we to interpret the relative stability of populations in natural communities?" A major advancement towards this interpretation was the development of multivariate statistical methods of vegetation ordination and classification (Whittaker 1978a, 1978b). These methods enabled multi-species community samples to be mathematically treated as single variables that could then be quantitatively related to environmental variables.

The interaction between communities and the environment creates ecosystems. In what may be considered the first actual ecosystem study, Mobius (1877) stated that, 'Science possesses, as yet, no word by which such a community of living things (oyster beds) may be designated; no word for a community where the sum of species and individuals, being mutually limited and selected under the average external conditions of life, have, by means of transmission continued in possession of a certain definite territory'. For such a community he proposed the term "biocoenosis". In Western science this concept has come to be known as the ecosystem, first coined by Tansley (1935). In North America, Forbes (1887) expanded on the work of Mobius, recognizing especially the relationship between predators and prey in a community and their relationship to the physical environment.

From consideration of community-environment relationships came the concepts of energy flow and material cycling. Thienemann (1926) described trophic levels in terms of producers and consumers and Elton (1927) described the ecological niche and the pyramid of numbers in terms of organization of the food chain. During the 1930s, Birge and Juday introduced the concepts of energy budgets and primary productivity (Juday 1940). The concepts of energy flows by trophic levels are credited to Lindeman, presented in his classic paper of 1942, 'The Trophic Dynamic Aspect of Ecology'. This paper 'did more than any other single contribution to bring concepts of energy flow to focus at the level of the ecosystem' (Odum 1968).

The cycling of nutrients between living and non-living components of the biosphere was brought to prominence by G. E. Hutchinson (1944, 1950) during the 1940s through his work on aquatic ecosystems. Material cycling studies of this type appeared earlier than similar studies on the terrestrial ecosystem because of the convenient use of the lake-land interface as an ecosystem boundary allowing, for the most part, only inputs of energy. Determining ecosystem boundaries for terrestrial biogeochemical studies posed greater difficulty. This was, however, overcome during the mid-1960s at the Hubbard Brook Experimental Forest in northern New Hampshire (Likens *et al.* 1967, Bormann *et al.* 1968, Likens *et al.* 1977, Bormann & Likens 1979).

To determine terrestrial nutrient inputs and outputs the small watershed approach was developed (Bormann & Likens 1969). This approach is based on using the watershed boundary as the ecosystem boundary. Thus, assuming no sub-surface leakage, the difference between materials that enter and materials that leave the watershed can be attributed to biotic activity within the ecosystem. Through these studies, it was possible to relate changes in the ecosystem nutrient budget to deforestation and ecosystem recovery.

With the realization that watershed boundaries could be used as ecosystem boundaries, it has become possible to correlate the functional aspects of community development with dynamics of energy flow and nutrient cycling. Although he was not aware of the functional nature of watershed-ecosystems, Evans (1956) recognized the landscape as a spatial arrangement of contiguous ecosystems: "The pathways of loss and replacement of matter and energy frequently connect one ecosystem with another'. More recently, Forman & Godron (1986) formally defined the landscape as 'a heterogeneous land area composed of a cluster of interacting ecosystems that is repeated in similar form throughout'. Just as the ecology of ecosystems cannot be understood without a minimum prerequisite knowledge of communities, the ecology of the landscape cannot be understood without a minimum prerequisite knowledge of ecosystems.

Landscape ecology, originally coined by the German geographer C. Troll (1950), began much earlier in Europe than in North America. In Europe, 'landscape ecology has gained general recognition as a branch of modern ecology, dealing as it does with the interrelations between man and his open and built-up landscapes' (Naveh 1982). More specifically, it is viewed as the scientific basis for the conservation of land which includes land planning, development, protection and reclamation (Naveh & Lieberman 1984).

By providing the scientific foundation for both natural and human-dominated land conservation, landscape ecology has overstepped the bounds of the purely natural sciences and has entered the realm of the human-based fields of study (eg. social and cultural sciences, economics, etc.) In Europe, this has resulted in a very broad interdisciplinary form of landscape ecology (see reviews of European landscape ecology by Naveh 1982, Tjallingii & de Veer 1982, Naveh & Lieberman 1984, and Naveh 1986).

The much younger form of landscape ecology currently developing in North America differs from the European form in two major ways according to Romme (1987). First, although it does have its applied aspects, the North American form is characterized by a stronger interest in 'fundamental questions about landscape pattern and function' apart from direct applications to land conservation. Secondly, European landscape ecology is concerned 'almost exclusively with human-dominated landscapes, whereas North Americans seem to have more interest in (and opportunity for) working with pristine landscapes as well'. Reviews of North American landscape ecology are provided by Forman (1981), Risser *et al.* (1983), Risser (1984), Forman & Godron (1986), and Urban *et al.* (1987).

A critical need at present for the incipient science of landscape ecology is well stated by Romme (1987) and is recognized by others (Forman 1983, Urban *et al.* 1987): 'if it [landscape ecology] is to mature into a legitimate science, as opposed to being only a tool of land planning and management, we must eventually be able to extract some emergent principles from our synthesis, some unifying ideas that are accessible only by thinking about heterogeneous landscapes themselves'.

This need may best be addressed through the application of newly developed methodology. Just as the thermometer, the logistic equation, ordination and classification, and the small watershed approach were critical methodological developments in the advancement of physiological, population, community, and ecosystem ecology, the development of remote sensing has facilitated the rapid and accurate quantification of landscape elements such as populations, communities, and watersheds (Naveh & Lieberman 1984, Botkin *et al.* 1984). In many cases it is even possible to measure more specific features such as biomass, density, and various levels of vegetation stress (Rock *et al.* 1986, Waring *et al.* 1986).

By using the small watershed approach for determining nutrient and energy budgets in combination with remote sensing for identifying and quantifying watershed-ecosystem biota, ecosystem level features can now be rapidly and accurately measured and related. This quantitative focus on contiguous watershed-ecosystems as landscape units will lead eventually to the emergence of principles unique to the ecology of landscapes.

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